

FUNCTIONAL MORPHOLOGY AND GEOGRAPHIC VARIATION IN THE DIGGING APPARATUS OF CURUROS (OCTODONTIDAE: *SPALACOPUS CYANUS*)

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We studied morphological and functional variations in jaws of coastal and mountain populations of subterranean *Spalacopus cyanus* inhabiting soils with contrasting hardness. We found almost no morphological differentiation between populations in the variables we measured. However, there were clear differences in incisor resistance between them. Apparently, soil hardness did not represent a selective pressure on cururos' digging apparatus. An Andean origin of this genus could explain our results.

Key words: functional ecology, morphology, morphometrics, Octodontidae, *Spalacopus*, subterranean rodent

Morphological and geographical variations within species are present in many groups of organisms (Best et al. 1986; Ellis et al. 1971; Murphy 1985; Owen 1989). In general, it is usually assumed that such variation is maintained by natural selection representing an adaptation to local conditions (but see James 1983). In addition, morphological studies could reveal selective factors that may be acting in a given habitat and could explain a phenotypic response to these factors (Arnold 1983; Lande and Arnold 1983). On the other hand, particular morphologies may limit ecological range of phenotype and in this sense may limit its geographical distribution (Ricklefs and Miles 1994 and references therein).

Subterranean mammals appeared around 55.6×10^6 years ago (early Eocene: Nevo 1995). Among them, and specifically in subterranean rodents, there is a great amount of functional and morphological convergence related to the specific characteristics of subterranean habitat and to changes associated with living and burrow-

ing in relatively permanent and sealed galleries (McNab 1966; Nevo 1979; Nevo and Reig 1990). This congruence is clearly evident when examining the morphological specializations associated with digging in different types of soils (Lessa and Thaeler 1989). That is, scratch or claw-digger species are often restricted to sandy soils, whereas chisel-tooth digger species have the potential to exploit a broader range of soils (Lessa and Thaeler 1989). There is, however, little knowledge about morphological changes among populations of a species that inhabits different soil types.

In this sense, the subterranean rodent *Spalacopus cyanus* (Rodentia: Octodontidae), the cururo, is a good candidate for assessing morphological divergence in the digging apparatus within species, because *S. cyanus* populations live in localities with different types of soil. In this study, we examined jaw morphology of coastal and mountain populations inhabiting soils with contrasting hardness. Coastal populations inhabit sandy soils, whereas mountain populations inhabit harder soils, therefore we predicted narrow and elongate rostra, pro-

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cumbent incisors, and wide zygomatic arches in mountain population. These characteristics of tooth-digging rodents (Lessa and Stein 1992) provide greater area for attachment of jaw muscles; variation in incisor procumbency could be related to different degrees of tooth digging. In addition, we also predict high bending strength in mountain population as a consequence of a greater use of incisors for digging.

MATERIALS AND METHODS

We examined skulls of 13 adults (6 males, 7 females) of *S. cyanus* from an Andean population (elevation of 1,600 m) in Lagunillas, central Chile (33°37'S, 70°18'W) and skulls of 20 (10 males, 10 females) from a coastal population (elevation of 20 m) in Con-Con, central Chile (32°56'S, 71°31'W). Skulls were obtained from the collection of the Museo Nacional de Historia Natural de Santiago (Chile) and represented all available samples. Body mass data were on specimens tags.

We assessed soil hardness at each locality with a soil compaction tester (Dickey-John Corporation, Auburn, Illinois). Data were obtained during spring and winter for coastal and Andean localities, respectively.

Ten cranial and dental measurements were taken to indicate relative shape of rostrum, zygomatic arches, and procumbency of incisors. They were measured to the nearest 0.1 mm with dial calipers (Fig. 1): basilar length of skull, zygomatic breadth, rostral width, rostral depth, rostral length, length of diastema, vertical length of incisors, width of incisors, depth of incisors, and distance from tip of incisor to base of 1st molar. Procumbency angles were computed by trigonometry according to Lessa and Thaler (1989).

Linear measurements were log-transformed for statistical analysis. We performed analysis separately for each sex, as we found significant differences between males and females in some variables.

One-way analysis of variance was applied to analyze differences in body mass between populations. Between the two populations both sexes differed in their body mass. For males, in the Andean population body mass was 95.7 ± 20.3 g (mean \pm SD) and in the coastal population, 77.6 ± 11.0 g ($F = 4.93$, $d.f. = 1, 14$, $P =$

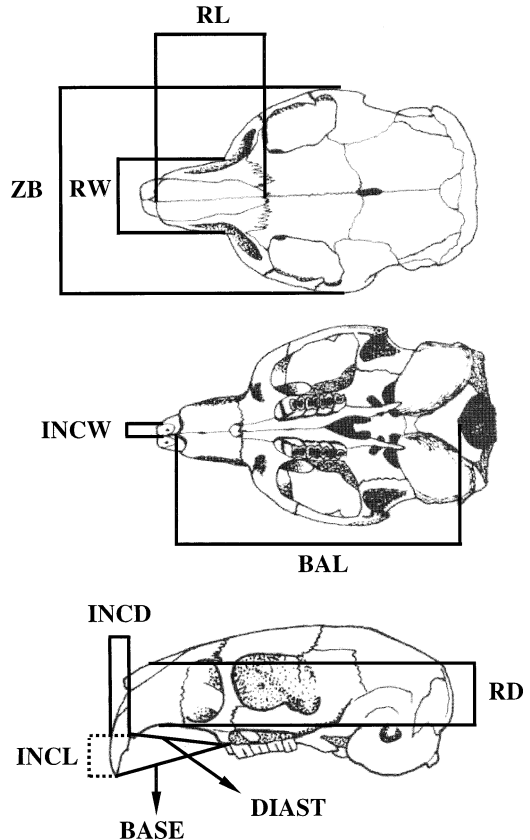


FIG. 1.—Measures used for morphometrics analyses: basilar length of skull (BAL), zygomatic breadth (ZB), rostral width (RW), rostral depth (RD), rostral length (RL), length of diastema (D), vertical length of incisors (INCL), width of incisors (INCW), depth of incisors (INCD), and distance from the tip of incisor to the base of 1st molar (BASE—adapted from Torres-Mura and Contreras 1998).

0.043). For females, in the Andean population body mass was 112.7 ± 31.6 g and in the coastal population, 74.0 ± 9.8 g ($F = 15.94$, $d.f. = 1, 15$, $P = 0.001$).

Because of differences in size within the sexes we used Burnaby's method for calculating size-independent principal components on the variance-covariance matrix as a way to uncover shape differences beyond the effect of body mass (Rohlf and Bookstein 1987). We removed variation related to size, not because size is unimportant but because we were interested only in shape change and size may obscure that variation (Humphries et al. 1981; James and

McCulloch 1990; Rohlf 1990; Zelditch et al. 1989). A stepwise discriminant analysis on the size-free data matrix of Burnaby analysis, performed on each sex, was used to discriminate between the 2 predefined groups (populations).

We used incisor length (INCL), width (INCW), and depth (INCD; Fig. 1) to test for differences in incisor strength between populations (each sex separately). We estimated basal cross-sectional area (CA) as $CA = \pi(INCW)(INCD)/4$ as a measure of resistance to shear stress, which seems to be large when teeth are loaded (Biknevičius et al. 1996). Thus, incisors with higher CAs will be more resistant to shear stress.

Incisors of rodents are sufficiently long relative to their basal diameter to be affected significantly by bending stresses. The resistance of incisors to bending stress depends on the force (F) applied on them, their section modulus (Z), which is a theoretical measure of cross-sectional bending strength, and INCL (Alexander 1989; Biknevičius et al. 1996). Therefore, the maximum bending strength (S) of incisors can be defined as $S = Z/(F)(INCL)$. As the magnitude of F applied was unknown, it was assumed to be 1 for both populations. Section moduli were estimated as

$$Z_x = \pi(INCW)(INCD)^2/32$$

$$Z_y = \pi(INCW)^2(INCD)/32$$

where Z_x and Z_y are section moduli about mediolateral and anteroposterior axes, respectively. Thus, S of incisors were estimated as

$$S_x = Z_x/INCL \quad S_y = Z_y/INCL$$

where S_x and S_y are indicators of strength of mediolateral and anteroposterior axes, respectively. Each measure was standardized by body mass raised to power of 0.67.

Statistical differences between populations were determined by the Mann–Whitney *U*-test for unpaired samples. Statistical analyses were done using STATISTICA® software (StatSoft, Inc. 1997) and the Burnaby's program by Norm MacLeod (<http://life.bio.sunysb.edu/morph/>).

RESULTS

Soil was much harder in the mountain location than in the coastal location. It was

$60,895 \pm 6,980.41 \text{ Nm}^{-2}$ (mean \pm *SD*) at the Andean site ($n = 68$) and $12,099.23 \pm 5,326.57 \text{ Nm}^{-2}$ ($n = 25$) at the coastal site. The difference between the 2 habitats was significant ($t = -32.20$, $P < 0.0001$).

Contrary to what we expected, there was no clear differentiation in shape between populations. Adjusted shape-vector scores on all combinations of the first 3 shape vectors show no clear separation between populations in either males or females (Figs. 2 and 3). For males, the first 3 Burnaby shape vectors of log-transformed covariance matrix accounted for 78.0%, 9.9%, and 4.3% of total variation, respectively. As these represent 92.1% of total variance there is no need to account for more than 3 factors. The 1st Burnaby-adjusted shape vector contrasted zygomatic breadth, rostral depth, rostral width, incisive depth, and incisive width with the basilar length of skull and other rostral measures associated with differences in incisor procumbency (length of diastema, rostral length, vertical length of incisors, and distance from the tip of incisor to the base of 1st molar). The 2nd Burnaby-adjusted shape vector contrasted the distance from the tip of incisor to the base of 1st molar and incisor length with rest of the variables. Finally, the 3rd Burnaby shape vector contrasted zygomatic breadth and incisor measures (length, width, and depth) with the other variables.

For females, the first 3 eigenvectors of the log-transformed covariance matrix accounted for 78.1%, 9.2%, and 4.6% of total variation, respectively. Together they represent 91.9% of total variance, indicating that no more than 3 factors need be considered. The 1st Burnaby-adjusted shape vector contrasted incisive length and width, diastema, and rostral length with rest of the variables. The 2nd Burnaby shape vector contrasted zygomatic breadth and length of incisors with other variables; whereas the 3rd Burnaby axis contrasted basilar length of skull, rostral length, length of diastema, and distance from the tip of incisor to the base of 1st molar with rest of the variables.

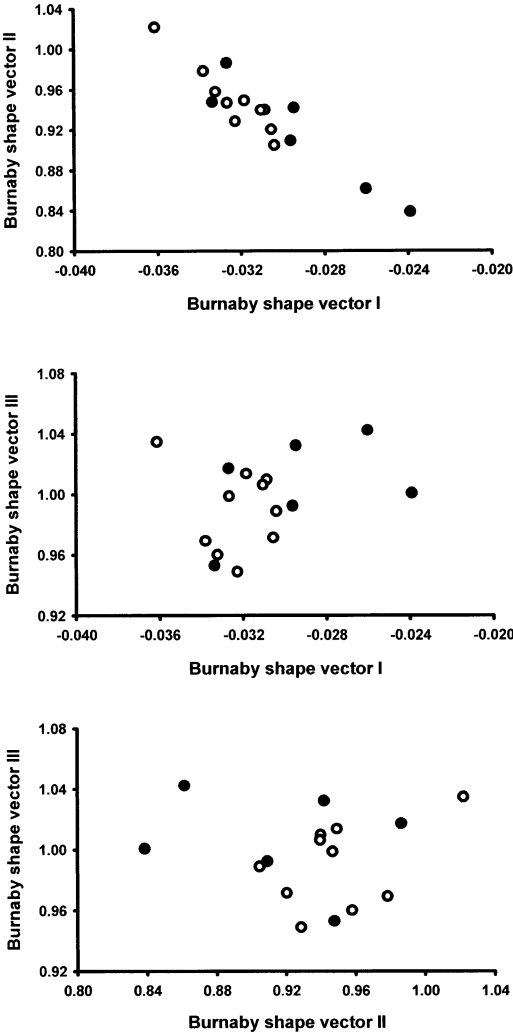


FIG. 2.—Mean scores of Burnaby shape vector in males showing that there is no clear separation between the 2 populations. Vectors represent multivariate shape beyond size effects. ● = Andean population, ○ = coastal population.

Adjusted shape-vector scores on all combinations of first 3 vectors (Fig. 3) show that there is no clear separation between females of the 2 populations.

For both sexes, discriminant analysis showed almost no shape discrimination between populations. For males, the 1st size-free discriminant function obtained accounted for 100% of total variation and was the only statistically significant function

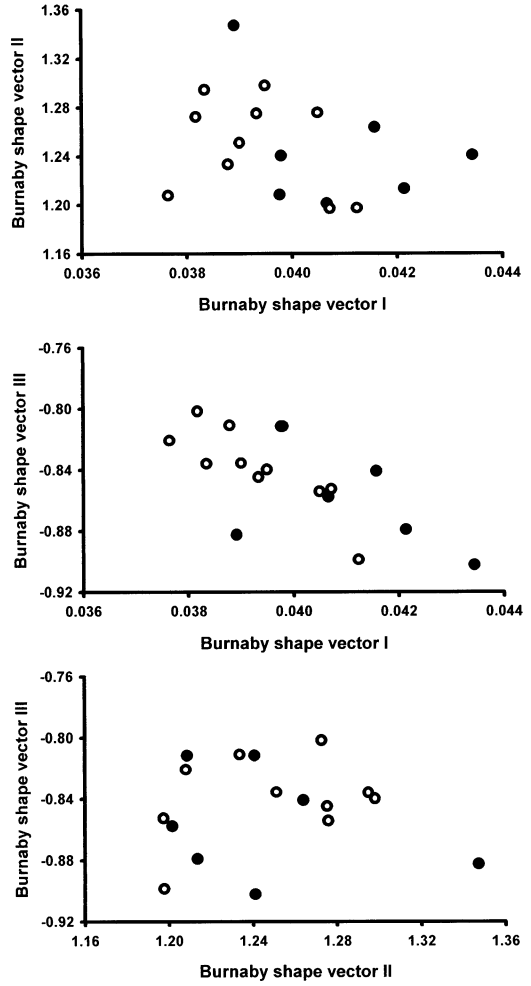


FIG. 3.—Mean scores of Burnaby shape vector in females showing that there is no clear separation between the 2 populations. Vectors represent multivariate shape beyond size effects. ● = Andean population, ○ = coastal population.

(Wilks' lambda = 0.5219, $F = 5.96$, $d.f. = 2, 13$, $P = 0.015$). Basilar length of skull (partial lambda = 0.5269, $P = 0.005$) and incisive depth (partial lambda = 0.7261, $P = 0.045$) were the variables that contributed to overall discrimination between populations. Fraction of correctly assigned individuals was 83.3% for the Andean population and 90% for the coastal population. For females, the 1st size-free discriminant function accounted for 100% of total variation and was the only statistically signifi-

TABLE 1.—Incisor strength as measured by cross-sectional area (measurement of resistance to shear stress) and maximum bending strength for coastal and Andean populations of *Spalacopus cyanus*. Mean values were compared between populations within each sex.

Population	<i>n</i>	Cross-sectional area (mm ²)		Maximum bending strength (×10 ² ; mm ²)			
				Mediolateral (<i>S_x</i>)		Anteroposterior (<i>S_y</i>)	
		\bar{X}	<i>SE</i>	\bar{X}	<i>SE</i>	\bar{X}	<i>SE</i>
Males							
Coastal	10	0.21	0.01	1.21*	0.06	1.07	0.06
Andean	6	0.20	0.02	0.98	0.11	0.87	0.10
Females							
Coastal	10	0.18	0.01	1.10*	0.06	1.00*	0.06
Andean	7	0.17	0.01	0.83	0.06	0.74	0.07

* $P < 0.05$, Mann-Whitney *U*-test.

cant function (Wilks' lambda = 0.5063, $F = 6.83$, $d.f. = 2, 14$, $P = 0.009$). Basilar length of skull (partial lambda = 0.5128, $P = 0.003$) and the length of diastema (partial lambda = 0.6151, $P = 0.010$) were the variables that contributed mostly to overall discrimination between populations. For females, 71.4% of the Andean and 70% of the coastal individuals were correctly assigned.

Contrary to what we expected, bending strength was greater in the coastal population (Table 1). Although populations did not differ in incisor shear strength (as determined by CA), they did differ in incisor bending strength (which varies not only with width and depth of incisor but also inversely with incisor length; Table 1). We found no differences in CA between males ($U = 25$, $z = 0.54$, $P = 0.588$) or females ($U = 32$, $z = 0.29$, $P = 0.770$) of the 2 populations. In particular, males of the coastal population had significantly higher mediolateral bending strength than males of the Andean population ($U = 11$, $z = 2.06$, $P = 0.039$). Coastal females had significantly higher values than Andean females for bending strength, both mediolaterally ($U = 9$, $z = 2.54$, $P = 0.011$) and anteroposteriorly ($U = 11$, $z = 2.34$, $P = 0.019$).

DISCUSSION

Morphological variation in digging structures of various species of subterranean ro-

ods has been found to be related to soil characteristics (Lessa and Thaeler 1989; Vasallo 1998). Generally, claw diggers are restricted to sandy soils, whereas chisel-tooth diggers are not. However, most studies have been limited to morphological variation among species, and there is almost no information about morphological change within species.

Our results show that populations of *S. cyanus*, although living in soils with contrasting hardness, are almost indistinguishable in morphology at least in the variables we measured. Contrary to our expectations, differences in soil type did not result in complete morphological differentiation between localities. A stepwise discriminant analysis showed nearly no shape discrimination between males or females of the 2 populations. In addition, discriminatory power of size-free functions is not high (males: Wilks' lambda = 0.5219; females: Wilks' lambda = 0.5063). Nevertheless, we must be cautious because the small sample size used (although the greatest available) coupled with the need to analyze each sex separately could also be reasons for not having found morphological differentiation (i.e., owing to low statistical power of the multivariate tests).

We found no differences in incisor shear strength, as measured by CA, between populations. However, there were clear differences in incisor resistance between popu-

lations, with the coastal population having greater bending strength (Table 1), a result we had not expected. Differences in bending strength can be obtained from differences in either section moduli (proportional to incisor width and depth) or incisor length. No differences between populations of either sex were found in section moduli, so differences must be related to differences in length. Probably differences in incisor bending strength are a consequence of differential use of incisors to dig. In particular, high altitude populations inhabiting localities with harder soils must use incisors frequently, and as a consequence, incisors must grow more than in the coastal (sandy soil) population. We suggest that differences in bending strength are related to longer incisors, which result from faster growth in the Andean population.

This kind of problem, the absence of morphological differentiation associated with digging in different types of soils, seems not to appear when we compare morphofunctional divergence among species of subterranean rodents. Numerous studies in pocket gophers have shown the existence of digging specializations associated with different ecological conditions (Lessa and Stein 1992; Lessa and Thaler 1989; Nevo 1999). In particular, Lessa and Thaler (1989) showed that *Geomys*, which has large claws and large forelimb muscles, is restricted to sandy soils, whereas the tooth digger *Thomomys*, with more procumbent incisors and forefeet muscles that are less robust than those of *Geomys*, inhabits a broader range of habitats. On the other hand, Vasallo (1998) showed that, although the small *Ctenomys talarum* is mainly a chisel-tooth digger, it performs quite well in sandy soils. Therefore, factors other than morphofunctional specializations, such as physiological characteristics and predation pressure which can constrain the presence of *C. talarum* in sandy soils must be taken into account to explain habitat preferences (Bush 1989; Vasallo et al. 1994).

Other studies on subterranean rodents

have dealt with morphological variation and ecological characteristics such as climate rather than soil type (Mathias 1990; Nevo et al. 1988). In particular, Nevo et al. (1988) related morphometrics to ecological and morphological changes during speciation of the superspecies *Spalax ehrenbergi*. Several studies have also examined possible abiotic causes for geographical variation in morphology among nonsubterranean rodents (Baumgardner and Kennedy 1993; Boyce 1978; Patton et al. 1979).

How can we explain the absence of morphological differentiation between coastal and Andean individuals? Contreras et al. (1987) suggested that the genus *Spalacopus* arose in situ, basing their hypothesis on its low species diversity and its morphological and physiological specializations to subterranean life. At the same time, recent information based on morphological and genetic characters suggest a recent origin of this genus, less than 5×10^6 years ago (M. H. Gallardo, in litt.), which is clearly after the uplift of the Andes (Brown and Lomolino 1998). In this respect, and given the almost indistinguishable morphology between both coastal and Andean populations, we suggest that *S. cyanus* originated in Andean localities and adapted to harder soils. Later populations, moving into coastal sandy soils, retained the original adaptation without morphological change. In general terms, this is in accordance with the idea that intraspecific patterns of morphological variation could suggest biogeographical hypotheses (Chernoff 1982). Morphological change within species represents a response to different selective factors in the environment (Arnold 1983; Ricklefs and Miles 1994). In this sense and according to our results, it seems that soil hardness did not represent an important selective factor in this species. In addition, it could be possible that coastal populations have the potential to exploit a broad range of soils.

Behavioral observations as well as morphological and functional analysis of forefeet and muscles could test whether Andean

and coastal populations have diverged in their digging specializations. In addition, claw and tooth diggers present a partial overlap in their morphological requirements, so conclusions based on just one component (i.e., skull or forefeet) could be misleading (Lessa 1990).

RESUMEN

Estudiamos la variación funcional y morfológica de la mandíbula superior de *Spalacopus cyanus* (cururo) tanto de poblaciones costeras como de montaña. Ambas localidades presentan suelos de distinta dureza. Las variables estudiadas no mostraron diferencias morfológicas entre poblaciones. Sin embargo, hubieron claras diferencias poblacionales en la resistencia de los incisivos. Aparentemente, la dureza del suelo no representa una presión selectiva en el aparato excavador del cururo. El origen andino de este género podría explicar nuestros resultados.

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